Nesom, G.L. 2015. Variants of *Erigeron divergens* (Asteraceae). Phytoneuron 2015-61: 1–24. Published 5 November 2015.
ISSN 2153 733X

VARIANTS OF *ERIGERON DIVERGENS* (ASTERACEAE)

GUY L. NESOM
2925 Hartwood Drive
Fort Worth, Texas 76109
www.guynesom.com

ABSTRACT

A distinctive variant previously identified as *Erigeron divergens* is recognized here as *Erigeron incomptus* A. Gray (synonym = *E. accedens* Greene) — it occurs widely in Arizona and into adjacent southwestern Utah, southwestern New Mexico and El Paso Co., Texas, and at least in northern Sonora and Chihuahua, Mexico. Apparently disjunct outliers occur in north-central California and northwestern Baja California. Plants of *E. incomptus* are perennial (flowering in the first year but eventually producing a woody caudex) with pinnatifid basal and lower cauline leaves with long petioles persisting after the blades are gone. *Erigeron incomptus* over its whole range is sympatric with typical, more widely distributed *E. divergens*, which is annual in duration and without the long-petioled, pinnatifid proximal leaves. Among annual plants of *E. divergens*, two variants are informally recognized: (1) those mostly single-stemmed from the base (typical *E. divergens*) and (2) those consistently with multiple stems from the base, all arising compactly from a caudex-like taproot apex. Chromosome counts of *E. incomptus* are triploid ($2n = 27$) and tetraploid ($2n = 36$); annual forms of *E. divergens* are reported as diploid, triploid, and tetraploid. Photos of specimens are provided as examples of the morphology of each of the three variant forms of *E. divergens* sensu lato, emphasizing variability in *E. incomptus*.

Erigeron divergens has long been viewed and treated as a polymorphic entity comprising morphological variants and a mixture of diploid and polyploid populations (e.g., Cronquist 1947; Nesom 2006 in FNANM). It occurs widely over the western USA and northwestern Mexico. A putative variant of *E. divergens* with prostrate, flagelliform runners, which Cronquist treated as *E. divergens* var. *cinereus* A. Gray, is segregated in the FNANM treatment as *E. tracyi* Greene (synonyms *E. colomexicanus* A. Nels., *E. dicladus* Greene; the name *E. nudiflorus* Buckl. has been misapplied to the species). Hybrids occur between *E. divergens* and *E. tracyi*, *E. flagellaris* A. Gray, and *E. modestus* A. Gray (*E. commixtus* Greene perhaps is a divergens-tracyi hybrid) but each of the species is in general morphologically distinctive. Whether hybrids occur among the three forms of *E. divergens* discussed below is not known.

Polyploidy and agamospermy apparently are common in *Erigeron divergens* and its close relatives and, along with hybridization, probably underlie the variability and apparent polymorphism characteristic, at least in part, of these species and hybrids. Diploids appear to be scattered through the range of *E. divergens*, at least in its southern part (reports in many references).

Three major morphological variants within *Erigeron divergens* sensu lato are found in its range in the southwestern USA. In the rest of the range (mostly northward), only the annual forms occur.

1. Annual plants essentially single-stemmed from the base (*Erigeron divergens* sensu stricto), with branches arising laterally from various points above the base but only uncommonly from near the very base (Figs. 1–3). This form occurs from Mexico north into western Canada.

Erigeron divergens Torr. & A. Gray, Fl. N. Amer. 2: 175. 1841. Based on *Erigeron divaricatus* Nutt., Trans. Amer. Philos. Soc. 2, 7: 311. 1840 [not *E. divaricatus* Michx. 1803]. **TYPE: USA**. Protologue: "Rocky Mountains, and plains of the interior of Oregon, Nuttall!" No

other data, *T. Nuttall 175* (holotype or lectotype: BM?; isotype: GH 6674, lower right plant, GH 6675 right plant).

Erigeron gracillimus Greene, Leafl. Bot. Observ. Crit. 2: 212. 1912. **TYPE: USA. Arizona.** [Coconino Co.]: Protologue: "Common on stony slopes, in forest of yellow pine, in the Coconino Forest Reservation, northern Arizona, the specimens collected 24 August 1911, by Jardine & Hill, who give 6800 feet as the altitude of the woodlands where it grows. On U.S. Herb. sheet 326788 are four good specimens of the same, distributed from the same general region, collected by M.E. Jones, 17 Sept. 1894. The special locality given for these is Nagle's Ranch." The description notes "Root annual, stem strictly erect, simple to near the summit." No syntypes found in available databases; not at NDG.

Erigeron furcatus Greene, Leafl. Bot. Observ. Crit. 2: 213. 1912. **TYPE: USA. Arizona.** Coconino Co.: San Francisco Mts, Kendrick's Park, 20 Aug 1889, *F.H. Knowlton 43* (holotype: US digital image!). Not at NDG.

Erigeron solisaltator Nesom, Madroño 28: 145. 1981. **TYPE: MEXICO. Chihuahua.** 0.5 km S of Rancho El Llano, flat (bottom of bolson), zacatal, 1185 m, 14 Jun 1973, *M.C. Johnston, T. Wendt, & F. Chiang 11317F* (holotype: TEX! digital image!).

2. Annual plants (sometimes short-lived perennial) with multiple stems from the base, all usually arising compactly from a caudex-like taproot apex, sometimes (in early season plants) bowl-shaped with decumbent-ascending stems and solitary heads topping unbranched stems (Fig. 4). Basal and lower cauline leaves are spatulate, the blades with entire or shallowly toothed margins. Plants of this form have a tendency to develop strongly woody taproots and a caudex with separated meristematic apices and in these respects are similar to *E. incomptus*, with which they may hybridize (Figs. 5, 6). The annual, "multicipital caudex" form occurs in northwestern Mexico into southwestern Texas, New Mexico, Arizona, and California. It is conceivable that the perennial *E. multiceps* Greene, which has this growth form, is a direct derivative of annual *E. divergens* (see comments in Nesom 2006).

Erigeron divergens (multi-stemmed from the base)

Erigeron deustus Greene, Leafl. Bot. Observ. Crit. 1: 211. 1906. **TYPE: USA. New Mexico.** [Catron Co.]: Mogollon Mts, West Fork of Rio Gila, ca. 7500 ft, 28 Aug 1903, *O.B. Metcalfe s.n.* (holotype: NDG digital image!).

Erigeron tephrodes Greene, Leafl. Bot. Observ. Crit. 1: 222. 1906. **TYPE: USA. California.** Inyo Co.: Foothills west of Bishop [protologue: "in moist grassy places near the house in "McGee's meadows"], 23 May 1906, *A.A. Heller 8315* (holotype:?; isotypes: CAS, F, GH, MO NY, P, PH, RENO, US-129072 and 129073). Digital images! of all types. No specimen at NDG. None of the collections cited here have the protologue locality details noted by Greene; a lectotype might be designated, but it seems likely that a specimen exists with these details.

Erigeron wootonii Rydb., Bull. Torrey Club 33: 153. 1906. Based on *Erigeron cinereus* var. γ A. Gray, Mem. Amer. Acad. Arts n.s. 4: 68. 1849. **TYPE: USA. New Mexico.** [Santa Fe Co.]: Protologue: "From the valley of Santa Fe Creek, near irrigating ditches; May to July. (385)." Label: 1847, *A. Fendler 385* (holotype: GH 6655 digital image!; isotype: GH 6656 digital image!).

Erigeron lavandulaceus Greene, Leafl. Bot. Observ. Crit. 2: 214. 1912. **TYPE: USA. Nevada.** [Douglas Co.]: Gardenville, 15 Jun 1902, *C.F. Baker 1085* (holotype: NDG digital image!; isotypes: CAS, GH, RM, RSA, US). Digital images! of all types.

3. Perennial plants (flowering in the first year from a slender taproot but eventually producing a woody taproot and woody, branching caudex) with pinnatifid basal and lower cauline leaves with long petioles persistent after the blades are gone (Figs. 7–19, Figs. 7–14 showing increasing development of a woody caudex). The pinnatifid leaves usually are crowded along 1–4(–8) cm of the stem base. Such plants, which I have annotated at various times and referred to (e.g., Nesom 2006) as the "*Erigeron accedens* form" of *E. divergens*, occur widely in Arizona and into adjacent

southwestern Utah, southwestern New Mexico and El Paso Co., Texas, and at least in northern Sonora and Chihuahua, Mexico. Apparently disjunct outliers occur in north-central California and northwestern Baja California (Map 1, Mexican localities other than Baja California not shown). The earliest name for the perennial form of *Erigeron divergens* is *E. incomptus* A. Gray.

In Arizona, *Erigeron incomptus* occurs at (1350–)2000–5000(–rarely to 6500) feet and flowers March–June, continuing sparsely into August and very rarely to October and November. Elsewhere it has been documented in flower as early as February and at elevations as low as 600 feet.

Erigeron incomptus occurs sympatrically with annual forms. Most chromosome counts of *E. incomptus* have been triploid, and apomictic seed production associated with triploidy in *Erigeron* probably contribute to its apparent morphological stability. Vouchers for triploid counts are shown in Figs. 16–19; a voucher for a tetraploid count is cited below from Doña Ana Co., New Mexico. The coherent geographical distribution in Arizona suggests that at least the triploids of *E. incomptus* had a single origin.

It seems likely that *E. incomptus* is of hybrid origin, the parental combination speculative. Whether the California and Baja California plants are long-distance disjuncts or of independent origin is not clear — typical *E. divergens* occurs in both areas but both areas are outside of the range of *E. flagellaris* and *E. tracyi*, which presumably are the closest relatives of *E. divergens* and among potential parents (if *E. incomptus* is a hybrid). Basal leaves in California and Baja California populations are unlobed but otherwise similar in morphology and placement to those eastward.

Plants apparently intermediate between *Erigeron incomptus* and annual forms are shown in Figs. 5–6. If they indeed are genetic intermediates, it suggests that tetraploid *E. incomptus* (capable of crossing with typical *E. divergens*) probably is more common than indicated by the limited sampling of chromosome numbers. Otherwise, it is possible that such plants are triploid *E. incomptus* showing further variation in the range of its expression.

The epithet *incomptus* (Latin, unadorned) alludes to the ray floret ligules much reduced in size (as in the type collection) — similar floral variants are known from other *Erigeron* species, including *E. flagellaris*.

Erigeron incomptus A. Gray, Synopt. Fl. N. Amer. 1(2): 218. 1884. *Erigeron divergens* forma *incomptus* (A. Gray) Cronq., Brittonia 6: 261. 1947. **Type: MEXICO. Baja California.** Carysito, 29 May 1883, *C.R. Orcutt 874* (holotype: GH digital image!; isotypes: NY digital image!, UC digital image!; possible isotypes: P-2 sheets digital images!).

The P specimens have as collection data only "Orcutt, 1883, Lower California," but they are closely similar to those at GH and NY and plausibly from the same collection.

Erigeron cinereus var. ß A. Gray, Mem. Amer. Acad. Arts n.s. 4: 68. 1849. **TYPE: USA. New Mexico.** [Santa Fe Co.]: Protologue: "Low, sandy banks of the Rio del Norte and of Santa Fe Creek; May to June. (380)." Label: 1847, *A. Fendler 380* (GH 6655, plant on right side of sheet). While "var. ß" is not a name, it seems useful to associate a specimen with the plant referred to by Gray.

Erigeron californicus Jeps., Bull. Torrey Club 18: 324. 1891. **TYPE: USA. California.** Sutter Co.: Marysville Buttes region, summit of South Peak, 20 Apr 1891, *W.L. Jepson s.n.* (holotype: JEPS 2569 digital image!; isotype: JEPS 2570 digital image!).

Erigeron cinereus var. *aridus* Jones, Proc. Calif. Acad. Sci. 2, 5: 695. 1895. **TYPE: USA. Utah.** [Washington Co.]: Protologue: "Washington, on sandstone rocks." Label: Silver Reef, gravel, 3500 ft, 3 May 1894, *M.E. Jones 5149v* (holotype: POM-RSA0001125 digital image!; isotype: US digital image!).

Erigeron accedens Greene, Pittonia 4: 155. 1900. **TYPE: USA. Arizona.** [Greenlee Co.]: Clifton, Apr 1899, *A. Davidson s.n.* (holotype: NDG! digital image!).

The *Erigeron* collections at ASU have been curated to reflect the distinction of *E. incomptus* from other expressions of the species. These records from Arizona can be found via SEINET (2015). Collections examined documenting the occurrence of *E. incomptus* in California, Utah, New Mexico, and Texas is provided here. From Baja California, I have seen only the type collection of *E. incomptus*.

California. Butte Co.: Berry Canyon (near Clear Creek), 6 May 1902, *Heller & Brown s.n.* (MO). Sutter Co.: Marysville Buttes, 17 May 1903, *Copeland 3234* (MO); Marysville Buttes, 22 Mar 1905, *Heller 7579* (MO); steep rocky slopes on S side of Marysville Buttes, in the *Quercus douglasii* belt, 15-16 Aug 1927, *Heller 14341* (MO-2 sheets). The type of *Erigeron californicus* is from Sutter County.

New Mexico. Doña Ana Co.: 1/2 mi W of Organ, S side of US-70, common in arroyo, 5000 ft, 16 May 1981, *Ward & Spellenberg 81-020* [voucher for *n* = 18] (TEX); Potrillo Mts, Mt Riley SE side, rocky slope, 23 Mar 1995, *Worthington 24206* (TEX); Potrillo Mts, W Potrillo Mts, road between El Paso and Columbus, 25 Mar 1955, *Worthington 24219* (TEX). Hidalgo Co.: 9 air mi SSW of Lordsburg, Pyramid Mts, W slope of Leitendorf Hills, rocky slope, 8 Apr 1984, *Worthington 11750* (TEX). Luna Co.: ca 9 mi WSW of Deming, S side of Red Mt, canyon and rocky slopes, 5200 ft, 13 Apr 1985, *Worthington 12990* (TEX).

Texas. El Paso Co.: Franklin Mts., 0.9 mi. W of jct Trans-Mountain Rd and Gateway South, 4300 ft, below road in arroyo, rhyolite alluvium, 28 May 1978, *Worthington 2881* (TEX); El Paso, NE part of city in yard of house at 10937 Whitey Ford, yard landscaped with crushed marble, 4 Sep 2010, *Worthington s.n.* (TEX).

Utah. Washington Co.: 5.2 mi NW of Toquerville, Browse Road on E flank of Beatty Hill, ca. 0.6 mi NW of Interstate 15, flats of volcanic rubble over brown clay soil, *Quercus turbinella* scrub community, burned in 2005, 4310 ft, 12 May 2012, *Fertig 27377* (UTC digital image!). Also see the type of *Erigeron cinereus* var. *aridus*, which is from Silver Reef in Washington County.

ACKNOWLEDGEMENTS

I am grateful to the staffs of TEX-LL, SMU/BRIT, and ASU — especially Walter Fertig at ASU for providing the photos of ASU specimens and for updating the ASU database (see SEINET) to reflect the new identifications of *Erigeron incomptus* (annotated at ASU as *E. accedens*, before associating the earlier name with these plants), to Barbara Hellenthal for checking the type status of specimens in the E.L. Greene herbarium at Notre Dame, and to John Strother for comments on the manuscript.

LITERATURE CITED

Cronquist, A. 1947. A revision of the North American species of *Erigeron*, north of Mexico. Brittonia 6: 121–302.

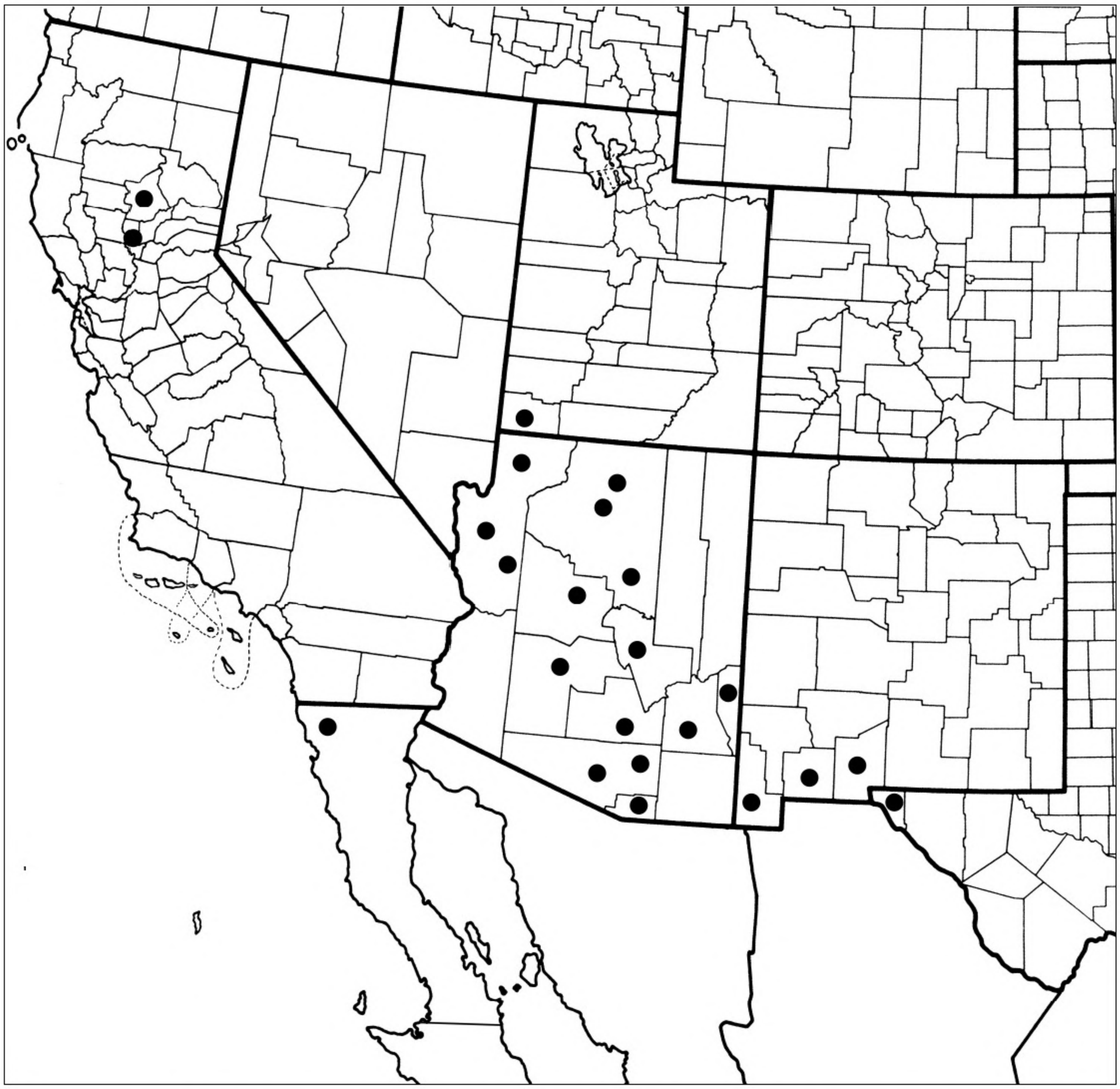
Nesom, G.L. 1992. *Erigeron* and *Trimorpha* (Asteraceae: Astereae) of Nevada. Phytologia 73: 203–219.

Nesom, G.L. 1992. Taxonomic notes on *Erigeron* (Asteraceae: Astereae) of California, Nevada, and Arizona. Phytologia 73: 186–202.

Nesom, G.L. 1993. *Erigeron* (50 species, 71 taxa). Pp. 253–261, in J. Hickman (ed.). Jepson's Manual of the Flora of California. Univ. California Press, Berkeley.

Nesom, G.L. 2006. *Erigeron* Linnaeus. Pp. 256–348, in Flora of North America North of Mexico, Vol. 20. Oxford Univ. Press, New York.

SEINET. 2015. Southwest Environmental Information Network. Managed at Arizona State Univ., Tempe. <http://swbiodiversity.org/seinet/>



Map 1. Distribution of *Erigeron incomptus* in the USA and Baja California, Mexico. It presumably should be expected to occur in southeastern Nevada. The range continues southward at least into Sonora and Chihuahua, Mexico.

Figure 1. *Erigeron divergens*, Yuma Co., Arizona, single-stemmed from the base.

Figure 2. *Erigeron divergens*, Yuma Co., Arizona, single-stemmed from the base.

ASU
191774
! Nesom 2015
FLORA OF ARIZONA
Greenlee County
California Polytechnic State University
Erigeron divergens Torrey & A. Gray
(Asteraceae)
White Mountains. T3N, R29E, S28. 2.5 mi S of turnoff to KP
Cienega along US Rte 666. Ca. 8900 ft elev. Forest of
Pinus ponderosa, Picea engelmannii, Abies concolor,
et al.
Rays pale purple, disk yellow. Local on roadside.
David Keil no. 23815
with Kathleen Keil
9 September 1992
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087072

Figure 3. *Erigeron divergens*, Greenlee Co., Arizona, single-stemmed from the base.

Figure 4. *Erigeron divergens*, Coconino and Cochise cos., multi-stemmed from the base.

Figure 5. *Erigeron incomptus* > *divergens*, Pinal Co., Arizona, multi-stemmed from the base, with woody, multicipital caudex similar to that of *E. incomptus*. Lower leaves entire with tendency for long, narrow petioles.

Figure 6. *Erigeron incomptus* > *divergens*, Santa Cruz Co., multi-stemmed from the base, with woody, multicipital caudex similar to that of *E. incomptus*. Lower leaves entire with tendency for long, narrow petioles.

Specimen entered in ASU Database
ASU
256902
cm
0 1 2 3 4 5 6 7 8 9 10
copyright reserved
ASU
Erigeron accedens
Nesom 2005
Erigeron divergens Torr. & A. Gray
Det. from duplicate Guy Nesom, 2002
Botanical Research Institute of Texas (BRIT)
Plants of Arizona
Flora of Seven Springs
ARIZONA STATE UNIVERSITY
Erigeron divergens Torr. & Gray
Family: Asteraceae
Arizona, Maricopa Co.; Tonto National Forest.
Between Seven Springs road and Camp Creek, near pull-off
stop just south of FS road 1509, N 33° 54.943' , W 111° 48.944'
Habitat: Chaparral. Elevation: 3400 ft. (1037 m)
Associated spp: Quercus turbinella, Juniperus coahuilensis,
Yucca baccata, Ferocactus cylindraceus, Acacia greggii,
Prosopis velutina.
Notes: Annual herb with purple rays.
Collected by: Shannon Doan 621 17 April 2001
with: D.Z. Damrel, A. Salywon
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087057

Figure 7. *Erigeron incomptus*, Maricopa Co., Arizona.

Erigeron accedens
Nesom 2015
HERBARIUM OF
THE NEW YORK BOTANICAL GARDEN
Plants of ARIZONA
Erigeron divergens T. & G. var. divergens
Det. K. Becker
PIMA CO.: Altar Valley, 8 airline miles south-southwest of Robles Junction (Three Points). T.17 S., R.10 E., Sec. 7. Elevation 2900 feet.
Creosote bush-mesquite-cholla desert; locally common in disturbed areas.
Rays pink, sometimes white with a pink tinge, disk yellow.
Noel H. Holmgren 6691 April 7, 1973
96071
HERBARIUM
ARIZONA STATE UNIVERSITY
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087058

Figure 8. *Erigeron incomptus*, Pima Co., Arizona.

Figure 9. *Erigeron incomptus*, Pima Co., Arizona.

Arizona State University (ASU)
267028
Vascular Plant Herbarium
Specimen entered in ASU Database
Erigeron accedens
Nesom 2015
Asteraceae of Arizona
Flora of Calcareous Outcropping/Horseshoe Dam
Erigeron divergens Torr. & Gray
Maricopa County: Tonto National Forest, Tonto National Forest, Lime Creek. N 33° 59.338', W 111° 44.073', 1996 ft., 609 m.
Creekside with Eriogonum trichopes, Bebbia juncea, Hymenoclea monogyra, Tamarix ramosissima, Mentzelia multiflora, Nicotiana obtusifolia var. obtusifolia, Erigeron divergens, Heterotheca subaxillarus, Conyza canadensis, Gaura mollis.
Plant height 2 feet; stems slightly pubescent, sticky: leaves alternated, linear; ray flowers lavender, disk flowers yellow.
10 November 2003
Dawn Goldman DG-40
with Joni Ward
Herbarium of Desert Botanical Garden (DES)
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087063

Figure 10. *Erigeron incomptus*, Maricopa Co., Arizona.

Figure 11. *Erigeron incomptus*, Pima Co., Arizona.

Figure 12. *Erigeron incomptus*, Pima Co., Arizona.

Specimen entered in ASU Database
Arizona State University (ASU)
263787
Vascular Plant Herbarium
Erigeron accedens
Nesom 2015
Erigeron divergens Torr. & Gray
Det. Liz Markings JAN 2007
Arizona State University (ASU)
Univ. Northern Colorado Herbarium (GREE)
AST
ARIZONA: PIMA CO.: On Arizona State Hwy. 86, ca. 6 mi. E of Sells; *saguaro* and *paloverde* dominant, very sandy soil. Elev.: 1082 m (3550 ft.)
W.E. Harmon 7099
19 Mar 1973
ASU Vascular Plant Herbarium Specimen Image Number
ASU0087064

Figure 13. *Erigeron incomptus*, Pima Co., Arizona.

Figure 14. *Erigeron incomptus*, Graham Co., Arizona. Basal and lower leaves are mostly entire, but note pinnate teeth on one leaf.

Figure 15. *Erigeron incomptus*, Gila Co., Arizona, *Little 4242* (ASU). Multicipital caudex with characteristic, numerous meristematic apices. The plant apparently was divided in half upon its collection for a specimen.

Figure 16. *Erigeron incomptus*, Yavapai Co., Arizona. Chromosome number $2n = 27$.

Erigeron accedens
Nesom 2015
Chromosome count from this plant
3 n = 27I
Determined by DAVID J. KEIL 1975
DET. Erigeron divergens T.&G. var. divergens
David J. Keil '75
Annotation - Herbarium of Arizona State University
Franklin College Summer Ecology Trip
PLANTS OF ARIZONA
Erigeron
Gila Co.: ca. 15 mi SE of Globe. Desert hillside. Rays white, disc yellow. Common on roadside.
David Keil no. 10794 1 June 1975
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087079
77121
HERBARIUM
ARIZONA STATE UNIVERSITY
2n = 27I

Figure 17. *Erigeron incomptus*, Gila Co., Arizona. Chromosome number $2n = 27$.

Chromosome count from this plant
3 n = 27 I
Determined by DAVID J. KEIL 1976
PLANTS OF ARIZONA
Herbarium of Arizona State University
Erigeron divergens T. & G. var. divergens
Pima Co.: Santa Catalina Mts.; 1.7 mi. below Molino Basin Campground on Mt. Lemmon Hwy. Rocky eroding granite slopes with Acacia, Prosopis, Baccharis, Haplopappus laricifolius, Yucca and Fouquieria. Ca. 4000 ft. elev. Common on roadside. Rays pale pink-purple; disc yellow.
T. Reeves & D. J. Keil K11355
30-IV-1976
ASU Vascular Plant Herbarium
Specimen Image Number
ASU0087081
Erigeron accedens
Nesom 2015
UNIVERSITY OF TEXAS HERBARIUM (TEX-LL)
Erigeron divergens Torrey & Gray
Det.: Guy Nesom, 1989
HERBARIUM
ARIZONA STATE UNIVERSITY

Figure 18. *Erigeron incomptus*, Pima Co., Arizona. Chromosome number $2n = 27$.

Figure 19. *Erigeron* aff. *incomptus*, Pinal Co., Arizona, perhaps a hybrid with *E. tracyi*. Chromosome number $2n = 27$.